Factors inducing the intense burrowing activity of the red swamp crayfish, Procambarus clarkii, an invasive species.

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SHORT COMMUNICATION

Silvia Barbaresi · Elena Tricarico · Francesca Gherardi

Factors inducing the intense burrowing activity of the red-swamp crayfish, *Procambarus clarkii*, an invasive species

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Abstract The burrowing activity of the invasive red-swamp crayfish, *Procambarus clarkii*, was studied along a 25-m-long transect in an irrigation ditch system in Italy. Our objective was to understand the factors inducing this species' intense digging, which can result in bank collapse and consequently in severe damage to both agricultural fields and natural ecosystems. Burrow morphology and position, together with their occupancy by crayfish and digging, were recorded once every 6 h for 10 consecutive days. The majority of burrows were simple, although a few had a chimney and were constructed at a farther distance from the water surface than simple burrows. Burrow occupancy and digging, together with their plugged/unplugged status, were constant throughout a 24-h cycle and were not related to any abiotic parameter of the habitat. Crayfish occupied and dug a burrow for a relatively short time (6 h on average). Once abandoned, old burrows were rarely reoccupied and often collapsed, while crayfish excavated new ones. As a result, the overall number of burrows increased. This massive use of banks by *P. clarkii* seems to be related to soil composition and humidity, which favour crayfish digging but also cause the easy collapse of burrows.

Introduction

Burrow construction by animals for feeding, reproductive, and defensive purposes can cause severe physical modifications of aquatic habitats in a process known as "physical ecosystem engineering", sensu Jones et al. (1997). Besides using natural shelters (Ilhéu et al. 2003), a large number of crayfish species dig burrows or burrow systems in soft substrates. The habit of burrowing is a main prerequisite for the invasiveness of non-indigenous species such as the red-swamp crayfish *Procambarus clarkii* (Huner 1977). The use of burrows allows this species to withstand environmental extremes (e.g., high temperatures and dehydration) and protects the crayfish from predators during sensitive phases of their life history (Huner and Barr 1991).

Although there are reports of complex structures (Gherardi 2001), most *P. clarkii* burrows are simple in their morphology (a single opening and a tunnel enlarging into a terminal chamber that hosts no more than two crayfish; Jaspers and Avault 1969). Mud plugs or chimneys in some instances stand over burrow openings (Correia and Ferreira 1995).

When digging is very intense, *P. clarkii*'s damage to agricultural fields (particularly to rice fields) and to natural systems can be severe, often causing bank collapse (Correia and Ferreira 1995). The impact of this species' burrowing on the habitat has been scarcely investigated, except for the increase of water turbidity followed by reduced light penetration and plant production (Anastácio and Marques 1997; Angeler et al. 2001).

The aim of the present study was to understand the factors that induce *P. clarkii*'s intense burrowing activity and thereby to identify the features that make a habitat more susceptible to damage from it. With this knowledge suggestions can be made for the conservation and management of freshwater habitats.

Materials and methods

The study was conducted near Florence, Italy (43°48′N, 11°12′E) during September 2000 for 10 consecutive days, in an irrigation ditch system composed of 1.5-m-wide canals. During this period, no rainfall occurred, water depth averaged 17–25 cm, oxygen content ranged between 12.4 and 54.6%, and mean pH was 7.

A 25×0.80-m transect along the bank of a canal was inspected by two researchers every 6 h, at sunrise (0500 hours), in daytime (1100 hours), at sunset (1700 hours), and at night (2300 hours). The 24-h cycle was consequently divided into four hour classes (i.e. 05–11, 11–17, 17–23, 23–05). Burrows (*n* from 57 to 100) were marked

S. Barbaresi · E. Tricarico · F. Gherardi (✉)
Dipartimento di Biologia Animale e Genetica,
Università di Firenze,
Via Romana 17, 50125 Florence, Italy
e-mail: gherardi@dbag.unifi.it
Tel.: +39-55-2288216
Fax: +39-55-222565

with numbered pegs and positions were noted using a grid reference system.

During every inspection, we recorded the number and position of new burrows and for each burrow

1. Its external morphology. Burrows were classified as "simple" (SB), "with a chimney" (CB; i.e. a turret-shaped mud structure), or "collapsed" (COL). SBs could be either open or closed by a crayfish-made muddy plug, whereas intact CBs were always plugged.
2. The distance of its opening from the water surface. The bank was subdivided into three vertical classes within a gradient of soil humidity (0–10 cm, >10–40 cm, and >40–80 cm above the water surface).
3. Whether it was occupied by at least one crayfish. To prevent disturbance to crayfish and damage to the burrow, we did not extract the occupant but defined as "occupied", OC (as opposed to "non-occupied", NO), those burrows (a) whose occupant was seen from the exterior, or (b) that showed fresh signs of digging (DG, as opposed to burrows without any sign of digging, WD), or (c) whose opening was plugged. "Just abandoned" were the burrows found vacant in a given inspection but occupied in the previous inspection. A control made in the same bank outside the transect showed that this classification corresponded to the actual presence/absence of crayfish inside burrows.

During every inspection, air, water, and burrow temperatures and dissolved oxygen content were measured, using, respectively, a mercury thermometer (inserted at 20-cm depth in a reference burrow for burrow temperature) and the portable oxygen meter Ati Orion (mod. 810). Due to its minimal variation, water level was measured once a day with a standard reference mark. At the end of the study, we analysed the soil composition of superficial (5-cm deep) substrate samples, which were collected from every 5-m-long segment of the transect and from every vertical trait of the bank, with a total of 15 samples. Samples were dried at 60°C for 24 h and then sorted using five sieves (63, 125, 500, 1,000, and 2,000 μm). Dry weight of each dimensional component was then expressed as a percentage of the total dry weight of the sample. The substrate was classified according to Wentworth (1922). Crayfish capability to excavate burrows was estimated by the Sc/Sg ratio (i.e. silt plus clay, divided by sand plus gravel in dry weight) as in Correia and Ferreira (1995).

For statistical analyses, we followed Zar (1984) and Siegel and Castellan (1988), using the software S-Plus 2000 (MathSoft Inc.). Differences between and among independent samples were examined using Student's *t*-test and a one-way analysis of variance (ANOVA), eventually followed by a Tukey test, or, when the assumptions for parametric analyses were not met, using the non-parametric Kruskall–Wallis ANOVA (statistic: *H*). *G*-test adjusted by William's correction was applied for frequency data (statistic: *G*) and Pearson correlations (statistic: *r*; after an arcsine square-root transformation to normalise percentages). To correct temporal autocorrelations arising from measurements repeated in time and to prevent temporal pseudoreplication, we used a repeated measures ANOVA (statistic: *F*; after having normalised percentages as above). To investigate the dynamics of burrow occupancy and digging, we analysed transitions between different categories of burrows. We compared observed and expected frequencies of transitions between two categories using the *G*-test. The expected frequency of the transition from, for example, category A to category B (transition AB) was computed from the overall frequency of A times the overall frequency of B divided by the frequency of all the recorded transitions.

Given are mean values ± standard error. The level of significance at which the null hypothesis was rejected is α=0.05. When no significant differences were found within a 24-h cycle, we analysed the hour class 23–05.

Results

External morphology and density of burrows

Of the overall 100 burrows marked, 11 were CBs and the remaining 89 were SBs. Openings were plugged in about 70% of SBs, without any difference throughout a 24-h cycle ($F_{3,32}$=0.679, P>0.05). Only 6% of burrows changed their morphology, mostly passing from SB to CB. Whereas the number of CBs remained almost constant (from 9 to 11), the density of SBs increased from 2.6 to 4 per m^2 (hour class 23–05: r_8=0.951, P<0.01).

Spatial distribution

Burrows, analysed for each category, were uniformly distributed ($G_4 \leq 3.945$, P>0.05). Their distance from the water surface remained constant (G_{18}=16.028, P>0.05), averaging 0–10 cm (each day analysed separately: always G_2>78.075, P<0.001). No burrow opening was ever found under water.

Whereas CBs were constructed farther from the water surface (19.23±3.15 cm, n=11) than SBs (8.69±1.27 cm, n=82; the last inspection: t_{89}=3.306, P<0.001), new (9.18±2.26 cm per day, n=7) and just-abandoned burrows (7.78±0.71 cm per day, n=9) were closer to it than OCs (15.66±0.39 cm per day, n=9; hour class 23–05: $F_{2,22}$=4.503, P=0.03; after Tukey test: OC>new=just abandoned). A similar pattern was found for DGs that were found at a lower distance from the water surface than WDs (9.88±0.99 cm vs 13.12±0.61 cm per day, n=9; $F_{1,16}$=7.698, P<0.01).

Substrate was mainly composed of silt (43%) and clay (44%), and to a lesser extent sand (13%). Its composition, that is, the Sc/Sg ratio, was uniform along the transect (H_4=8.20, P>0.05) and throughout the bank (H_2=2.54, P>0.05).

Burrow occupancy

NOs decreased (hour class 23–05: r_8=–0.752, P<0.02) and COLs increased with time (r_8=0.954, P<0.01; Fig. 1). Burrow occupancy, that is, the percentage of inspections in which the same burrow was found occupied, did not vary throughout a 24-h cycle ($F_{3,335}$=0.37, P>0.05).

The duration of a continuous occupancy of a burrow and the time between two subsequent occupancies were analysed in classes of frequency for all burrows, except for those that were always or never occupied during the study and those whose beginning or end of occupancy was unknown. Most burrows were continuously occupied for 6 h (G_{24}=326.549, P<0.001). After being abandoned, a few were reoccupied after, most often, 12 h (G_3=124.607, P<0.001). The overall time each burrow was occupied ranged between 12 and 222 h, the average and the mode being 100±11 h (n=46) and 24 h, respectively.

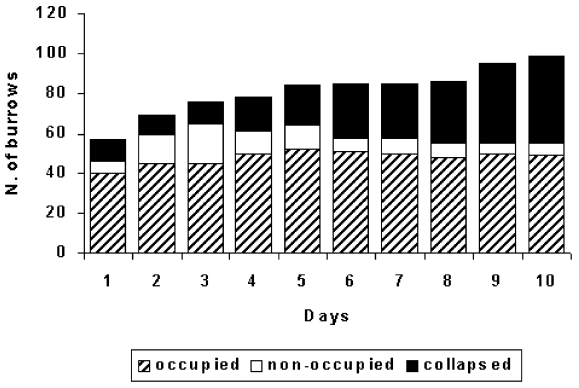

Fig. 1 Number of occupied, non-occupied, and collapsed burrows plotted against time

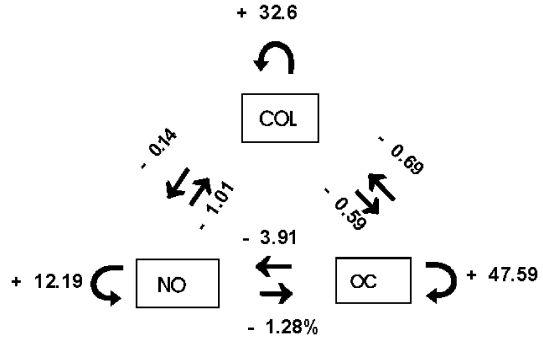

Fig. 2 Transition analysis between categories of burrows, that is, *OC* (occupied), *NO* (non-occupied), and *COL* (collapsed). *Numbers* represent the observed frequency (%) of each transition; plus and minus mean that transitions have observed frequencies significantly ($P<0.05$) higher and lower, respectively, than expected

The dynamics of burrow occupancy was studied by analysing the transitions between three categories, that is, (1) OC, (2) NO, and (3) COL for the burrows followed for at least 3 days, excluding those always or never occupied or always collapsed. Transitions between different categories were significantly less frequent than expected, whereas transitions within each category were more frequent ($288.531<G_1<19.553$, $P<0.001$) (Fig. 2).

Digging activity

Digging activity, that is, the percentage of inspections in which the same burrow was recorded as DG, was constant throughout a 24-h cycle ($F_{3,335}=0.239$, $P>0.05$). The duration of continuous digging and the time between two consecutive bouts of digging were analysed in classes of frequency for all the burrows except for those always or never dug during the study and those whose beginning or end of digging was unknown. The most frequent class of continuous digging was 6 h ($G_9=338.851$, $P<0.001$). A few burrows were subject to further digging after a pause of, most often, 12 h ($G_{17}=161.224$, $P<0.001$).

Fig. 3 Transition analysis between burrows with (*DG*) and burrows without (*WD*) signs of digging. See Fig. 2 for details

Burrows classified as DG (or WD) at a given inspection did (or did not) show signs of digging at the subsequent inspection more frequently than expected, whereas transitions between the two categories of burrows were less frequent ($126.047<G_1<11.327$, $P<0.001$; Fig. 3).

Abiotic parameters

As expected, air, water, and burrow temperatures and dissolved oxygen content significantly varied throughout a 24-h cycle ($F_{3,34}$ always >5.169, $P<0.005$). The external morphology of burrows and their occupancy were not correlated with any abiotic parameters of the habitat (always $r_{7-34}<0.464$, $P>0.05$). Digging activity showed a significant decrease with the distance from the water surface (hour class 23–05: $r_7=-0.825$, $P<0.01$).

Discussion

In many countries, damage to agricultural fields caused by *P. clarkii*'s burrowing activity has made this species achieve pest status (Hobbs et al. 1989). In the study area, possibly due to soil composition (mostly silt and clay), we recorded intense excavation by crayfish, the density of simple burrows increasing from 2.6 to 4 per m^2 in 10 days. The high rate of digging (together with burrow occupancy and plugged/unplugged status) did not vary throughout a 24-h cycle, as also revealed by other studies describing either *P. clarkii*'s burrowing ecology (Gherardi and Barbaresi 2000; Gherardi et al. 2002; Ilhéu et al. 2003) or its use of space and general activity (Gherardi et al. 2000a, 2000b; S. Barbaresi et al., unpublished).

Consistent with the present study are the findings by Correia and Ferreira (1995) that burrow density (0.07–6.8/m^2) increased with the amount of fine sediment in the soil. In fact, crayfish seem unable to construct permanent burrows in soils with large particles, that is, sand, gravel, and cobbles (Grow and Merchant 1979; Grow 1982; Hobbs and Whiteman 1991; Ilhéu et al. 2003). The presence of free water has an additional documented effect on the crayfish's burrowing ability (Grow and Merchant 1979; Grow 1982; Hobbs and Whiteman 1991). Our results show that, although soil composition was uniform throughout the bank, burrows were mostly excavated at a distance of 0–10 cm from the water surface (see also Correia and Ferreira 1995), where moist sediments may favour crayfish digging.

A spatial segregation between burrows of different morphologies was, however, found, burrows with a chimney being located at a greater distance from the water surface than simple burrows. As previously suggested for other species (Williams et al. 1974), plugged chimneys prevent evaporative water loss from the burrow, which is related to the soil drought process, and, therefore, to the distance from the water surface.

In addition to favouring burrow construction, moist sediment, together with soil composition, seems to make vacant burrows easy to collapse, as showed by the increased frequency of collapsed burrows. In fact, (1) burrows closer to the water surface are more often subject to restoration than those located farther away, (2) digging activity is more intense at higher water levels, and (3) occupied burrows are more distant from the water surface that those vacant.

The increase with time in burrow density can be the result of either a higher number of crayfish in the study area, or their tendency to construct new burrows at the end of their wandering or foraging movements (Gherardi et al. 2000b) but not to reoccupy the abandoned ones. The second hypothesis seems to be supported by the augmented number of collapsed burrows and by the results from transition analyses.

A possible scenario is that, in this habitat where soil composition and moist sediment cause the easy collapse of the abandoned burrows but also favour crayfish excavation, the construction of new burrows is less expensive in terms of time and energy than the restoration of old ones. This could explain the massive use of banks by *P. clarkii*, as shown from the number of newly excavated burrows, the short time of burrow occupancy, and the intense digging activity. Obviously, our conclusion should be supported by other studies in different habitats and areas. Additional data are in fact required to formulate a general rule of habitat susceptibility to *P. clarkii's* invasion.

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